9-2013

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JOURNAL OF PALEONTOLOGY

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Journal of Paleontology, 87(5), 2013, p. 818–825

0022-3360/13/0087-818$03.00
DOI: 10.1666/12-152

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ABSTRACT— Strophomenid brachiopods have long been interpreted as "snowshoe" strategists, with their flattened concavo-convex valves providing resistance to foundering in very soft sediments. There has been a sharp difference of opinion in whether the shells were oriented with their convex or their concave surface in contact with the sediment. This study, along with independent evidence from sedimentology, ichnology, and morphology, indicates that the strophomenids lived with their shells concave down (convex up). Experiments indicate the force required to push shells into soft cohesive muds is much greater for the convex up than for the convex down orientation. Forces also increase with shell curvature. All measured forces greatly exceed estimates of the downward force exerted by the weight of the shell, indicating that foundering resistance may not have been the key functional requirement. Instead, a convex up orientation would have provided resistance to overturning in currents, in particular if the valves gaped widely. The "snowshoe" may not be the relevant paradigm for the shell morphology of these forms. An alternative is that they functioned more as a tip-resistant base, similar to those of garden umbrellas or stanchions.

INTRODUCTION

STROPHOMENID BRACHIOPODS (Strophomenoidea), with their discoid, flattened, often concavo-convex shells are the archetypical Paleozoic "snowshoe" strategists (Rhoads, 1970; Thayer, 1975). Most strophomenate lineages, in particular strophomenids, are characterized by the loss of the pedicle in adults and the adoption of a free-living on soft-substrates life style (Alexander, 1975; Williams and Carlson, 2007). That these brachiopods were adapted but not obligated to muddy seafloors seems inescapable. *Rafinesquina*, for example, is an abundant form characteristic of Cincinnatian Ordovician faunas, and is often found preserved as sparse shell pavements in mudstones (Dattilo et al., 2008) as well as articulated specimens in shelly or comminuted-shell limestones (Dattilo et al., 2009, 2012).

Although there is general consensus that these forms were recumbent on the seafloor, there has been debate, at times heated, on whether these brachiopods were oriented convex down or convex up in life. This debate has centered on which orientation would function better to prevent sediment fouling of the brachiopod feeding mechanism (Lamont, 1934). Many authors have strongly supported a convex-down position to hold the commissure above the sediment-water interface (Lamont, 1934; Rudwick, 1970; Richards, 1972; Alexander, 1975; Bassett, 1984; Leighton and Savarese, 1996; Leighton, 1998), with the convex-up position predicted to produce passive burial of the commissure and consequent loss of functionality. Preservation in the convex-up position was interpreted as post-mortem reorientation to a more stable position (Richards, 1972; Alexander, 1975).

The tendency of dead strophomenid shells to passively reorient was supported by experimental studies by Alexander (1975) and Savarese (1994). Alexander (1975) placed weighted plaster models of *Rafinesquina alternata* in a flume with a fine sand bottom. Five shape classes were used for the models as well as two or three size classes. In general, models overturned from a convex-down to a convex-up position in velocities of 1–3 m/s. Flat forms overturned more readily than alate and geniculate forms. Similarly, Savarese (1994) utilized a flume to measure drag forces on various taxa of concavo-convex brachiopods as a function of orientation. Drag was greater on shells in the convex-down position and increased with geniculation of the shells.

Several sets of experiments using model shells and focusing specifically on life orientation were described by Leighton and Savarese (1996). Additional flume experiments confirmed that drag was higher for convex-down orientations and geniculate morphologies. They also determined that sediment scour and transport was greatest around more geniculate shells. Of particular relevance to the current study is that they placed a variety of specimens on two carbonate mud substrates (25% and 50% water by volume) in both convex-up and convex-down orientation and then observed the extent to which they sank into the substrate over a 48-hour period. Not surprisingly, the commissures (anterior margin) of all shells oriented convex-up became completely or partially buried. For shells oriented convex-down, results depended on substrate firmness and degree of geniculation. On the less fluid mud, none of specimens sank in. On the more fluid substrate, flatter specimens with low surface area to volume ratios sank in sufficiently to bury their commissures, but more geniculate specimens were able to keep their commissures elevated above the substrate. Leighton (1998) showed that this proposed relationship is consistent with greater geniculation of *Rafinesquina* specimens from muddier intervals in the Richmondian of Indiana.

The alternative convex-up orientation was supported by Pope (1976) and Lescinsky (1995) based predominantly on the locations of epibionts. Lescinsky further argued that the seafloors may have been firmer than usually interpreted, with shells thus less likely to sink. He also suggested, albeit without evidence, that the convex-up orientation may actually have been advantageous in clearing the interior of material. The epibiont

evidence was dismissed by Leighton (1998, 2005) as being inconclusive.

A new line of evidence was introduced by Dattilo (2004) who observed sedimentary structures adjacent to specimens of *Sowerbyella* that were interpreted as trace fossils produced by these brachiopods during reorientation within the sediment, consistent with at least a limited ability to move. The suggested mechanism was valve clapping, caused by rapid contraction of the adductors (Rudwick, 1970). This interpretation was vigorously criticized by Leighton (2005), which was responded to by Dattilo (2005). In a later paper Dattilo et al. (2009) described moats, or depressions in the sediment, surrounding the commissure of convex up specimens of *Rafinesquina* from numerous localities in the Cincinnatian. These were construed as resulting from rapid valve snapping, which cleared sediment from the margins.

Implicit in previous interpretations of both orientations is that strophomenids, akin to modern terebratulids, had a relatively narrow gape between the open valves. Morphological studies now strongly suggest that strophomenids had relatively wide gapes (Hoel, 2007). For example, in *Rafinesquina* (Dewing and Dattilo, 2008), the relative positions of the fulcrum and the attachment points of the diductor between the myophore (on the cardinal process) of the dorsal valve and the anterior-extending muscle scar of the ventral valve would have allowed a maximum gape of approximately 45°, an angle that is comparable to the "back stop" angle in the hinge mechanism, suggesting that the wide gape was habitual. The ability to actively clear sediments from the commissure is clearly an adaptation to prevent sediment fouling of the lophophore. A wide feeding gape would also have prevented fouling in any orientation by fostering slow inhalant currents and by drawing water from well above the sediment water interface. For this reason, a concave-down life orientation would not have prevented a strophomenid from feeding.

The common thread of these arguments is that, no matter what the orientation, the role of the flattened concavo-convex strophemenid shape was to maintain a viable position on the substrate using the snow-shoe strategy. The theoretical foundation for this strategy comes from a seminal paper by Thayer (1975) that provided a general equation for the forces controlling the maintenance of a stable position on the surface of soft sediments. The static stress σ exerted downwards by an organism on the sediment can be expressed as:

$$\sigma = (\rho_{org} - \rho_{water}) \frac{S_2}{nS_1} rg$$

where ρ_{org} is the density of the organism; ρ_{water} is the density of the fluid, r is the characteristic linear size of the organism; S_1 is a shape factor that relates r to the organism's total surface area A ($A = S_1 r^2$); n is the fraction of that surface area that is in contact with the surface (the bearing area), S_2 is a shape factor that relates r_{org} to the volume ($V = S_2 r^3$) and thus the mass; and g is the acceleration due to gravity. As discussed by Thayer, this equation predicts that an organism can reduce its downward stress by reducing its density ρ_{org}, including by partial burial to increase buoyancy; by becoming smaller (reducing r); by increasing S_1 relative to S_2 by making the organism flatter; or increasing n by partially burying it (the latter two constitute the "snowshoe" adaptation suggested for strophomenids). Despite the clear conceptual structure provided by the Thayer model (1975), however, there has been little in the way of direct measurements of the actual resistance to sediment penetration by organisms suggested to be immobile suspension feeders on soft-sediment (Thayer, 1979).

In this paper we assess whether strophomenids were snow-shoe strategists, and if so, how did shell shape or orientation impact the ability to withstand sinking? In particular, we describe experimental studies of the force required for strophomenid brachiopod shells to penetrate soft sediments as a function of size, shape, and orientation. Our results are more in keeping with a convex up rather than a convex down life orientation, consistent with other lines of evidence that support this interpretation. These outcomes also indicate, however, that resistance to foundering into soft sediments and thus the snow-shoe strategy may not have been the principal control on morphology of these forms.

MATERIALS AND METHODS

In order to test a wide range of sizes and shapes (Table 1), 22 loose specimens of *Rafinesquina* were selected from previous collections made from several localities representing several stratigraphic horizons within the Upper Ordovician (Katian) rocks of the Cincinnati region in Ohio, Indiana, and Kentucky. Additional collections were made for this study to find the smallest and largest specimens possible. Specimens smaller than 25 mm are very rare in limestones and are not known to endure weathering from shales, so juvenile shells were not tested. In addition to the *Rafinesquina* specimens, five specimens of *Strophomena* were collected. All specimens had weathered from mudstone, so specimens associated with limestone (both genera) are not represented. In some cases, only one disarticulated valve was present.

We use "concave" or "convex" to refer to the form of the outer surface of the conjoined valves. *Strophomena* is a resupinate strophomenid, where the ventral valve is concave and secondarily thickened and the dorsal valve is convex, whereas *Rafinesquina* has a concave and thickened dorsal valve and a convex ventral valve (Lescinsky, 1995). Following previous authors, we will refer to both forms as concavo-convex, but it should be kept in mind that "convex up" or "convex down" does not refer specifically to dorsal or ventral valves, but only to the orientation of the convex valve. Measurements taken on each specimen include (Fig. 1): width of the hinge line (WH), plan view chord length along the median (CL), plan view maximum width (W), and maximum depth (D). We also measured the length of a string placed directly on the convex surface along the median of the shell (arc length; AL). The ratios of Width/Depth (WD=W/D) and Length/ArcLength (LA=CL/AL) were used as measures of the relative curvature of the shells. We will use curvature in preference to geniculation, since geniculation refers to abrupt changes in shell curvature (Williams and Brunton, 1997); we are measuring the amount, but not the shape of the curvature (Bloom et al., 2008).

For each specimen, we measured the forces needed to penetrate the sediment at a constant velocity in both concave up and concave down orientations. Experiments were performed with a soft mud substrate prepared from kaolin and water (other runs, not discussed here, were on fine sand). Because of evaporation, it was difficult to maintain consistent water content of the sediment among runs. As a result, we standardized our results by measuring the forces on a flat brass disc at both the beginning and end of the runs. The brass disc had a plan area and outline similar to that of a strophomenids (width=49. 4 mm; length= 41.6 mm). All reported forces are relative to those on the disc. This approach also removes the direct role played by different sizes or masses of shell; we are only looking at the influence of shape.

TABLE 1—Dimensions and relative forces in soft mud for specimens examined. Measurements as shown in Fig. 1. Orientation: convex down or convex up. Forces measured relative to that of flat brass control disk. Submerged weights estimated from dry weight and dimensions of shells (see text).

Genus	Specimen	Width hinge (mm)	Max. width (mm)	Length (mm)	Depth (mm)	Arc length (mm)	Mass (g)	Force/control		Submerged weight (N)
								Down	Up	
Brass disc	Control		49.4	41.62				1	1	
Rafinesquina	LB48-1	49.0	52.7	40.8	10.2	48.5		1.37		
Rafinesquina	LB48-2	34.2	40.7	34.3	11.5	45.8	12.6	1.08	1.9	0.031
Rafinesquina	LB48-3	51.0	52.1	41.4	5.3	46.5		1.26		
Rafinesquina	LB48-4	45.2	48.9	40.0	10.5	49.5	18.7	1.42	2.39	0.046
Rafinesquina	LB48-5	30.6	43.6	36.4	9.5	42.5	12.1	0.83	2.05	0.030
Rafinesquina	RAF236-A1	27.6	31.0	25.4	4.3	40.5	9.3	0.88	1.46	0.023
Rafinesquina	RAF236-A2	33.2	35.9	34.1	8.0	50	15.1	1.35	2.35	0.037
Rafinesquina	RAF239	43.0	43.1	37.5	7.8	42.5	9.5	1.03	1.67	0.023
Rafinesquina	RAF245	34.3	36.3	28.5	13.3	44	17.7	0.94	2.05	0.043
Rafinesquina	RAFLB-4	41.2	52.2	42.3	13.9	55	26.3	1.7		0.064
Rafinesquina	SF361-10	42.6	45.0	40.6	12.4	52	16.8	1.41	2.5	0.041
Rafinesquina	SF391B-17	36.6	38.1	35.7	12.5	47.5	8.7	0.83	1.93	0.021
Rafinesquina	SF391B-19	47.8	51.0	42.6	10.2	50.5	16.5	1.97	2.56	0.040
Rafinesquina	SF391C-14	40.9	41.0	33.7	7.1	40	9.5	1.21	1.43	0.023
Rafinesquina	SF391C-17	42.0	42.0	34.2	9.4	42.5	10.4	0.99	2.02	0.025
Rafinesquina	TFK-90	29.5	29.9	29.2	10.3	40.5	6.2	0.57	1.33	0.015
Rafinesquina	TW100-1	31.1	34.6	29.4	6.6	34.5	4.2	0.41		0.010
Rafinesquina	TW100-2	33.7	38.3	31.3	9.7	41.5	8.6	0.87	1.64	0.021
Rafinesquina	TW100-3	32.5	35.8	30.2	7.9	37.5	5.4	0.78	1.17	0.013
Rafinesquina	TW100-6	32.4	37.7	32.5	9.7	40	5.7	0.88	1.37	0.014
Rafinesquina	TW100-7	24.5	32.8	26.8	7.2	32	4.5	0.59		0.011
Rafinesquina	TWDNT-1	47.6	48.4	36.1	12.0	47.5	13.8	1.39	2.07	0.034
Strophomena	STROP237	32.9	33.7	24.8	6.2	44		0.48	0.67	
Strophomena	STROP242	29.1	29.1	18.0	6.4	30.2	2.4	0.27	0.37	0.006
Strophomena	STROP242-1	30.9	30.9	19.4	7.8	26	3.8	0.33	0.56	0.009
Strophomena	STROP242-2	25.1	25.1	15.9	4.9	19.5	1.4		0.26	0.004
Strophomena	STROP242-3	24.1	24.1	17.1	8.2	24	3.0		0.34	0.007
Strophomena	STROP245	34.3	36.3	28.5	13.3	44	12.3	0.76	1.4	0.030

Forces were measured using a Chatillon DFIS-10 digital force gauge, mounted on a Chatillon TCM-200 motorized test stand. The motorized test stand moves the force gauge at constant downward velocity, pushing the attached specimen down at a continuous rate. Specimens were attached to the gauge by a brass rod hot glued at the center of the dorsal or ventral valves. Most runs were done at a vertical velocity of 5.1 cm/minute (2 inches/minute setting), although some were repeated at 10.2 cm/minute. Data was recorded using Chatillon Nexygen DF software and uploaded into SYSTAT (ver. 13) for analysis. For each run, we documented the peak compressional force (recorded as negative values in Newtons) measured until the upper surface of the shell was coincident with the top of the sediment surface (Fig. 2). In some runs, we also tracked the force as a function of depth; in these cases, we converted time to depth of penetration. These runs were done at speed of 2.54 cm/minute (1 inch/minute). Measurements were repeated four times at different locations on the substrate for each specimen. In some cases, we reused the same specimen in two different runs; in these cases we report the average of the results (which were

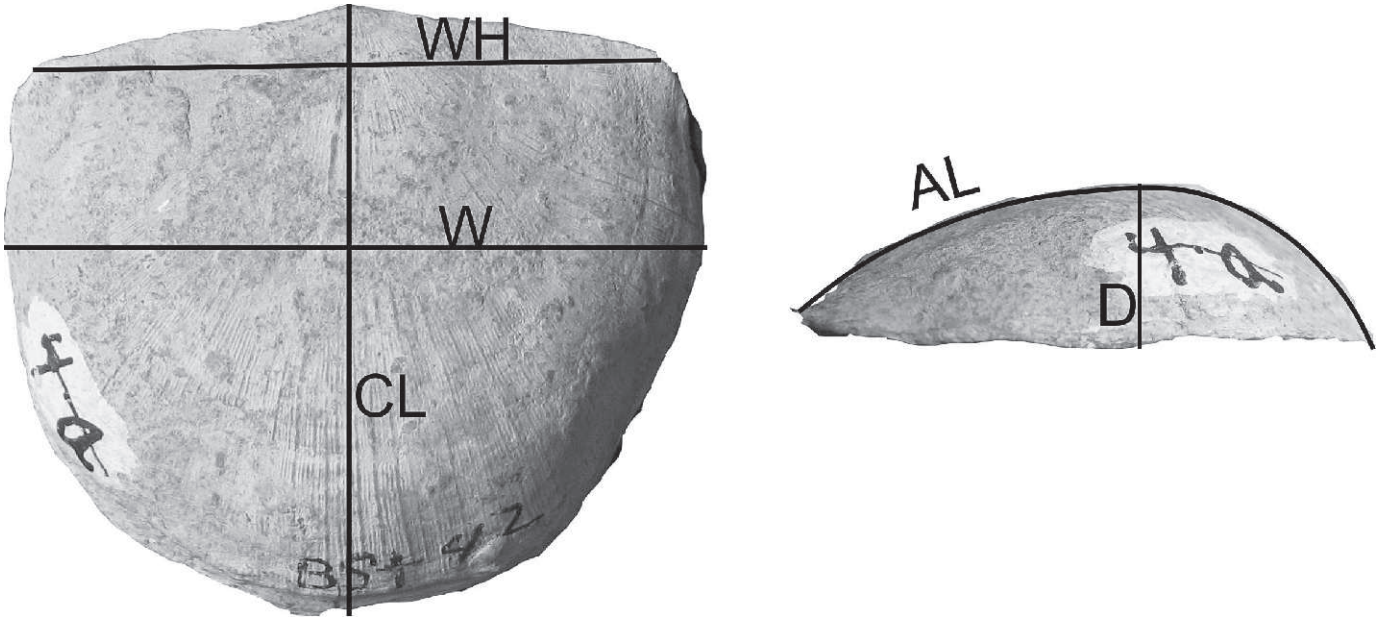

FIGURE 1—Measurements (mm) taken on brachiopod valves. Abbreviations: WH=width of the hinge line; W=maximum width; CL=chord length; D=maximum depth; AL=arc length.

FIGURE 2—*Rafinesquina* shell in convex-up orientation being pushed down into soft kaolin mud.

very close). In cases where one of the valves was missing, we measured only relevant up or down forces.

Since shells are not actively being pushed into the sediment, the most relevant force value is the weight of the living organism in its shell. To determine this, the mass (g) of the preserved shells was obtained on an OHAUS Adventure Pro analytical balance (Table 1). If it is assumed that both the original shell and any infilling are calcitic, dividing the mass by the density of calcite (2.71 g/cc) gives the approximate volume of shell and infill and thus the total mass of water displaced by the animal. A sectioned specimen was used to estimate that 40% of the volume was occupied by original shell, with the remainder being calcite infill and thus the original internal volume. An average density of 1.027 g/cc was used for the combination of viscera and seawater occupying the internal volume. Together, these measurements allowed the rough calculation of the original mass and weight in air, the buoyancy, and thus the original net downward force exerted by the living organism. The calculated values for submerged weight in Newtons are in the last column of Table 1. Note that we believe that the estimate for the percent volume of shell is conservatively high, so the submerged weights are possibly overestimates.

RESULTS

The maximum penetration forces on the soft mud for the control disc was an average of 0.87 Newtons (n=6; s.d.=0.06) for a penetration speed of 5.1 cm/s; the results for the higher speed were virtually identical (mean =0.91 N; n=6; s.d.=0.07). The maximum penetrative force relative to that of the control disk for convex up and convex down orientations is shown in Fig. 3.1 for *Strophomena* and Fig. 3.2 for *Rafinesquina* and given in Table 1. For brachiopods with both dorsal and ventral valves, the forces for both orientations are plotted; if a single valve is present, only a single point is given. Also shown are linear regressions through the data.

For both orientations, the forces required to penetrate the sediment are greater than those of a flat disk of the same plan area. This is certainly because the actual wetted surface area of shell in contact with the sediment is greater due to the curvature of the valves. It is also clear that the force required to push a shell into the mud is higher for convex up shells for both taxa over the entire range of sizes. On average, the required downward force in the convex up orientation is 1.75 times higher than that in the convex down orientation for the same brachiopod (n= 21, s.d.=0.35).

As would be expected, the required force scales with size, represented by the maximum width. The regression of relative force on width is significant for both orientations of *Rafinesquina* and for *Strophomena* in the convex-up orientation (there is insufficient data for *Strophomena* in the convex-down orientation). The slopes of the relationships are also nearly identical within the given standard errors (Table 2), although there is a great deal of scatter around the lines.

Much of this scatter may represent the role of shell curvature. This was explored by performing multiple linear regressions where the independent variable was force and the predictor variables were maximum width (W) and the ratio (LA) of chord length (CL) to arc length (AL). Flat shells would have an LA value of 1.00; LA decreases with increased shell curvature. As shown in Table 2, the R^2 values of the regressions noticeably increase when "curvature" is included.

This can be further explored by looking at the residuals of regressions of relative force on width. These residuals are thus more-or-less size independent. Figure 4 plots these values against LA, the measure of curvature. This graph shows that for shells in both the convex up and convex down orientations, penetration resistance increases as shell curvature ("geniculation") increases. The correlation coefficient *r* for both is about the same (0.52). This implies that penetration resistance increases not only with overall size, but as wetted shell area increases relative to plan area, whether in convex up or convex down orientation.

The forces discussed above are maximum values, produced by pushing the shell into the sediment until it is buried parallel to sediment-water interface and then documenting the maximum value. We also conducted a series of runs in which we recorded the increase of force with time of penetration. All of these runs were conducted at a constant downward velocity of 25.4 mm/minute (1 inch/minute setting), which was then converted to approximate depth below the surface by estimating when the shell first contacted the sediment surface (e.g., 10 seconds after initial penetration the shell reached a depth of 4.2 mm). Representative runs for one of the brachiopods in the convex up and convex down orientations are shown in Figure 5. Because of the uncertainty of when the shell first contacted the mud, not all of the runs intersect the 0,0 point on the axes.

The plot shows clearly the difference in force needed to penetrate soft sediment in the convex up versus the convex down orientation. It also shows that in both orientations, the force is linear with depth (time). This is comparable with studies on mechanical properties of modern marine sediments (Bokunkiewicz et al., 1974). The maximum forces shown here and in Figure 3 are in the neighborhood of 1 to 2 Newtons. Forces in experiments with fine sand substrates were an order of magnitude greater. In comparison, the average submerged weight of the strophomenid shells was 0.25 N, far smaller than these forces.

DISCUSSION

Concavo-convex strophomenid brachiopods are among the most common Ordovician organisms. As of October 2012, the Paleobiology Database included 15439 brachiopod occurrences belonging to 558 genera. Of these, *Rafinesquina* is the most common genus (1295 occurrences, 8.4% of total) and *Strophomena* the fourth most common (731 occurrences, 4.7% of the total; the second and third most common are *Zygospira* and *Dalmanella*). Even if these represent "garbage can taxa"

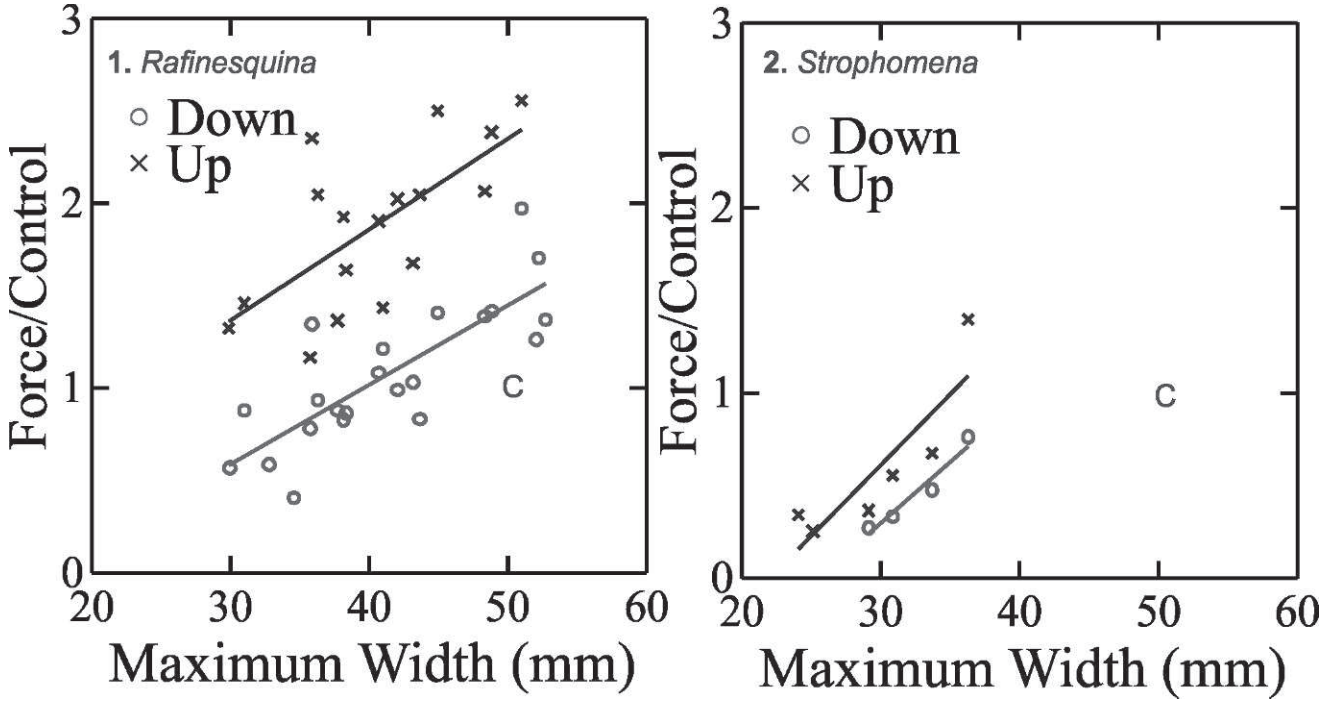

FIGURE 3—Maximum forces required to penetrate soft mud relative to flat brass disc (C) for convex up and convex down orientations as function of maximum shell width. Same specimens were used for both orientations. *1*, *Rafinesquina*; *2*, *Strophomena*; only three specimens of *Strophomena* were articulated. Average force for the control disk was 0.9 N.

(Plotnick and Wagner, 2006), the body form itself is still extremely abundant. This makes it more than worthwhile to produce an accurate reconstruction of their life habit.

Previous studies are somewhat contradictory. Although they clearly indicate that the convex up position is hydrodynamically more stable, the perceived necessity of keeping the commissure above the sediment water interface forced the conclusion that the life position was convex down. One implication of this is that living brachiopods that were overturned must have smothered and died. This further suggests that these animals must have lived in quiet water. An additional implicit assumption is that the substrate was quite soupy, so that sinking into the sediment and fouling of the filter feeding apparatus were serious problems for the organisms. A final assumption is that of a fairly narrow gape, so that access to the interior of the shell was small and constrained to be near the sediment-water interface, with corresponding risks of drawing in large amounts of sediment and clogging the lophophore.

The current study suggests that sinking into the sediment was most effectively prevented by being in the convex up orientation, coupled with increasing shell curvature. However, prevention of foundering into soft-sediment may not have been the major functional control on the orientation of the forms. The presence of preserved moats around convex up *Rafinesquina* (Dattilo et al., 2009) indicates not only was the organism capable of clearing the area around its shell, but that the sediments themselves were relatively cohesive. Sedimentological aspects of the Cincinnatian mudstones strongly indicate that sediment influx was sporadic and that, as a rule, mud was quite firm by the time that the brachiopods occupied it (Dattilo et al., 2008, 2012). Likewise, the skeletal sands and gravels associated with Cincinnatian limestones probably furnished a solid base. The downward force measured on sediment exerted by the weight of these brachiopods, in either orientation, was an order or two of magnitude smaller than the forces necessary to penetrate soft muds and additional order of magnitude smaller than that necessary for fine sands. This also indicates that shape, rather than mass was the major control on sediment penetration, and that sinking wasn't a problem unless sediments were much soupier than we believe.

As indicated before, morphological evidence indicates that the potential gape of these brachiopods was relatively wide. In addition, as mentioned by Lescinsky (1995), the concave valve is much thicker than the convex valve in both *Rafinesquina* and *Strophomena*, despite these being different valves anatomically. This is so prevalent that most deposits of disarticulated valves contain significantly more concave than convex valves. Taken together, this suggests an alternative functional interpretation and reconstruction.

Figure 6 shows cross sections of *Rafinesquina* on relatively firm sediment surfaces in both convex up and convex down interpretations. The shells are gaped at the 45° angle suggested

TABLE 2—Regressions of relative force on maximum width, and on both maximum width and ratio LA of length to cord length, a measure of shell curvature; s.e.=standard error.

		Force ratio on width							Force ratio on width, "curvature"	
Genus	Orientation	n	Slope	s.e. slope	Intercept	s.e. intercept	R^2	*P* value	R^2	*P* value
Rafinesquina	Down	22	0.043	0.007	−0.699	0.299	0.64	0.000	0.771	0
	Up	17	0.049	0.014	−0.118	0.565	0.46	0.003	0.712	0
Strophomena	Up	6	0.076	0.022	−1.678	0.665	0.75	0.026	0.786	0.099

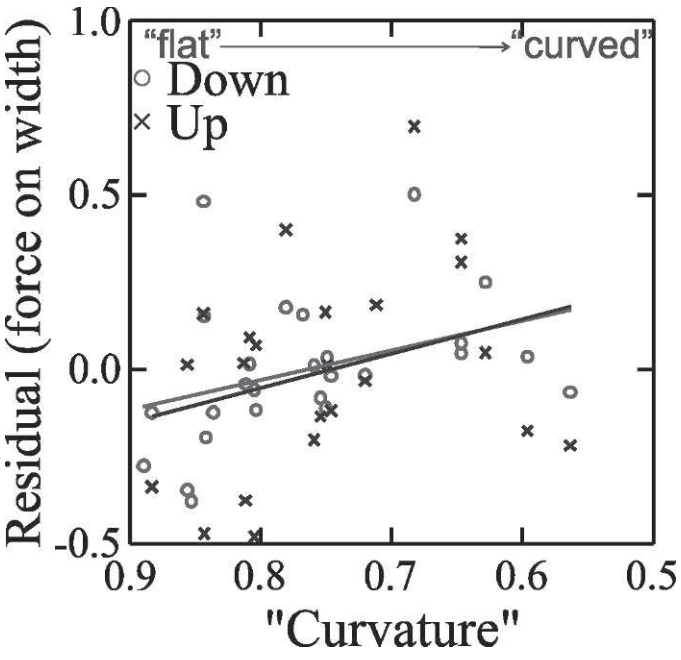

FIGURE 4—Residuals of regression of relative force on maximum width plotted against ratio LA of chord length (CL) to arc length (AL). LA is a measure of shell curvature, with high values representing flat shells (maximum LA=1.0). Note that horizontal axis is reversed, so that more curved shells are to right. For the convex up orientation, r=0.53; for convex down, r=0.52.

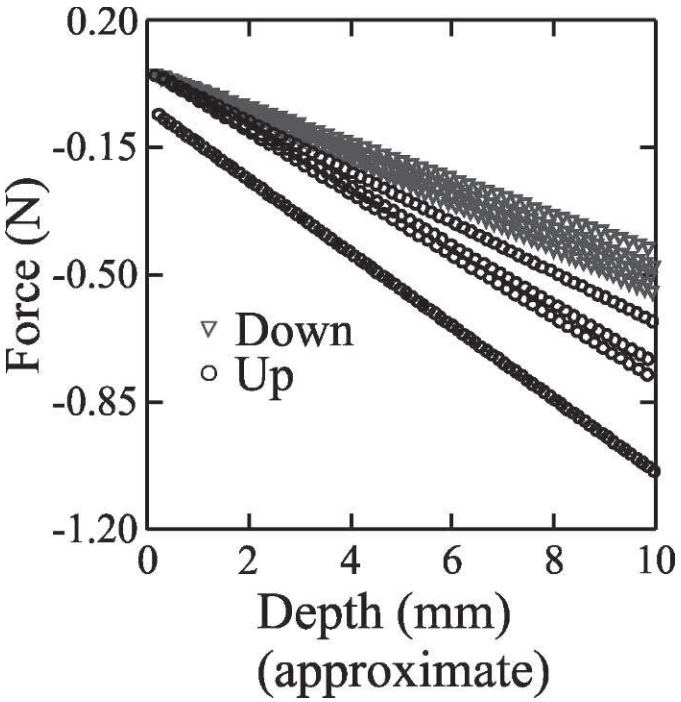

FIGURE 5—Force versus distance diagrams for brachiopod SF391C-17 in convex up and convex down orientations. Distances are approximate from the sediment –water interface and are converted from seconds after contact. Forces are compressive. Graph cutoff at depth sufficient to bury (shell depth is 9.41 mm). Dots are data points, lines are linear regressions fit to the data.

by the morphology of the muscles attachment and the hinge. As the shells open, the center of gravity of the organism would be shifted toward the hinge. In the case of the convex down orientation, this would rock the shell backward (towards the hinge), since there is no countervailing force except friction with the shell margin. This would be enhanced if there were currents, since the shell gape raises the shell margin into a high drag position well out of the boundary layer and nearly perpendicular to flow. In contrast, in the convex up orientation the entire perimeter of the shell, including commissure and hinge, which lie within a single plane, is in contact with the sediment. Shifting the center of gravity backward would press the shell margin down into the substrate and movement would be resisted. The upper valve would also not be raised as high above the seafloor or perpendicular to flow. This reconstruction is also compatible with the thicker valve being lower and would function equally well on mud, sand, or shell gravel substrates.

Our data also indicates that increased shell curvature, even in the absence of abrupt geniculation (e.g., *Leptaena*) does make a positive contribution to shell stability, in either orientation. This is compatible with the relationship with sediment mud content observed by Leighton (1998).

CONCLUSIONS

Biomechanical methods are a key tool for functional analysis, but are as subject to refutation as any other types of functional argument and are just as sensitive to underlying assumptions and alternative interpretations. Functional analyses of fossil forms should be based on multiple lines of evidence when available, including taphonomic, ichnologic, and sedimentary evidence, as well as careful biomechnical studies (Plotnick and Baumiller, 2000). In this we disagree with Leighton (2005) who argued that biomechanical evidence needs to have paramount importance in interpreting the functional morphology of extinct organisms. The evidence described in this paper, in addition to the earlier evidence from sedimentology, ichnology, morphology, and epibionts, indicates that a valid reconstruction for adult *Rafinesquina*, *Strophomena*, and similar strophomenids is convex up and with a wide gape. This does not preclude the possibility that the organisms were viable in a convex down orientation, but we believe that the preponderance of the evidence makes this less likely. It should also be stressed that our interpretation of *Rafinesquina* and *Strophomena* may not apply to all strophomenids. For example, the flatness, abrupt geniculation, and long trail of the convex ventral valve of *Leptaena* suggest that it may have formed a stable base (Hoel, 2005). *Leptaenoidea* is often cemented to hard substrates by the ventral valve (Hoel, 2007).

Finally, despite the appeal of the snowshoe paradigm (Thayer, 1975), it may not actually have been the limiting functional requirement. The strophomenid shape generated far more resistance to sinking in either orientation than required by the weight of the shell, in particular if the sediments were relatively cohesive or coarse. A possible alternative paradigm is that of a tip resistant base, such as those placed under a drinking cup or supporting a garden umbrella. Placing the concave shell downward would have stabilized the shell in currents, even if the valves remained gaped for feeding. Although the paradigm approach (Rudwick, 1964) may be very useful for the development and preliminary testing of functional hypotheses, biomechanical testing and consideration of alternative paradigms is essential before a particular interpretation should be accepted.

ACKNOWLEDGMENTS

We thank the researchers who collected the brachiopod collection data and the members of the Paleobiology Database (paleodb.org) who compiled them. D. L. Meyer made valuable suggestions. We are grateful to reviewers I. Percival and O. A.

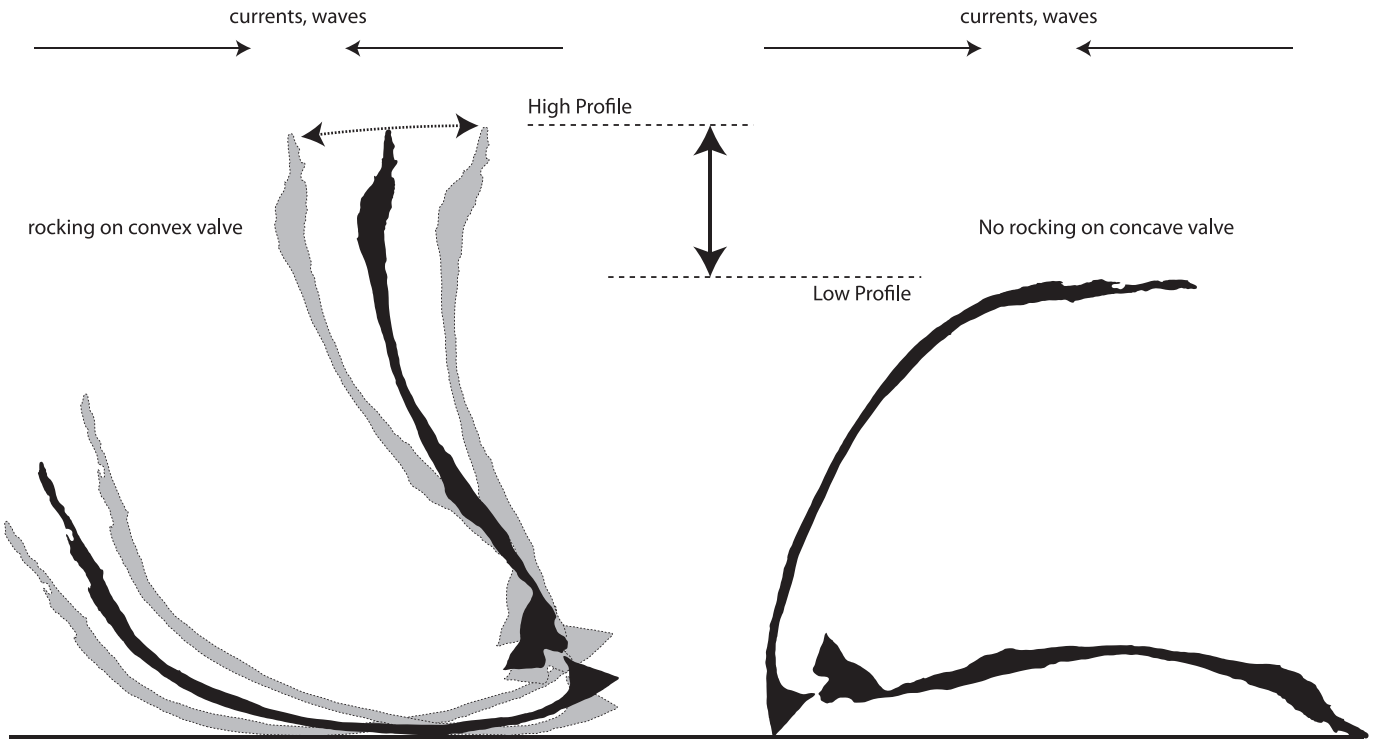

FIGURE 6—Cross-section reconstructions of *Rafinesquina* with wide gapes in both convex down (left) and convex up (right) reconstructions. It is assumed that the substrate is relatively firm. In both cases, the opening of the valves moves the center of gravity of the organism towards the hinge. In the convex down orientation, this would tend to rock the shell backward. In the convex up orientation, the posterior margin of the shell is pressed against the sediment, preventing movement. The convex down orientation increases the distance of the raised valve from the sediment surface relative to that of the convex up orientation, elevating the shell margin out of the boundary layer and exposing it to higher current velocities.

Hoel for their helpful comments on the manuscript. This material is based upon work supported by the National Science Foundation under EAR 0921771. Any opinions, findings, and conclusions or recommendations expressed in this material are those of the authors and do not necessarily reflect the views of the National Science Foundation.

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ACCEPTED 7 MARCH 2013